

# Notes on the Reproductive Strategies of the South African Vermetid Gastropods *Dendropoma corallinaceum* and *Serpulorbis natalensis*

BY

ROGER N. HUGHES

Department of Zoology, University College of North Wales, Bangor, Gwynedd LL57 2UW, United Kingdom

## INTRODUCTION

THE PRESENT PAPER discusses the adaptive significance of the reproductive methods employed by *Dendropoma corallinaceum* (Tomlin, 1939) and *Serpulorbis natalensis* (Mörch, 1862) in the light of new data on juvenile respiration rates, energy reserves and dispersal capabilities, together with the general biological information on these species described in HUGHES (1978a, 1978b).

*Dendropoma corallinaceum* is a dominant organism of exposed rock faces in the cooler waters of the Cape Province of South Africa, being replaced by a very similar species, *D. tholia* Keen & Morton, 1960, in warmer waters from the Transkei northwards. *Dendropoma corallinaceum* builds sheet-like colonies over the rock surface and on vertical faces the colonies form a zone about 1 m wide centred on LWS. Upper limits to this zone are set by desiccation and lower limits are often set by competition with the limpet *Patella cochlear* Born, 1778. *Serpulorbis natalensis* has the same geographical distribution as *D. corallinaceum* but occurs in loose aggregations beneath stones and on the sides of boulders below LWS in fairly sheltered water. It is replaced by the broadly similar species *S. aureus* Hughes, 1978 (HUGHES, 1978c) in the Transkei.

## MATERIALS AND METHODS

During August–November 1975, *Dendropoma corallinaceum* and *Serpulorbis natalensis* were kept in the laboratory, during which time they produced large numbers of young, making it possible to measure juvenile respiration rates and to collect material for subsequent biochemical analysis. From these observations it was possible to esti-

mate the energetic cost of the pre-settlement dispersal phase and to compare this with the energy reserves of the newly hatched young.

## ANIMALS

*Dendropoma corallinaceum* was collected from the upper edge of the *Patella cochlear* zone (MLW) at Miller's Point on the Cape Peninsula. Lumps of the reef-like colonies were chipped off the rock face and placed in a well-aerated aquarium at ambient air temperature. Crawling young emerged from the colonies within 24 h but the hatching rate declined over several weeks. The adults survived and sustained normal feeding activities for 4 months. *Serpulorbis natalensis* were collected from the undersurfaces of stones within 1 m below MLW on the southern (lee) side of Schaapen Island, Langebaan. Crawling young emerged within 24 h, continuing to emerge for 2 weeks.

The aquarium was cleared of young at 21:00 h and the freshly hatched young that had accumulated by 08:00 h the next morning were collected and placed in the respirometer.

## RESPIROMETRY

A Gilson differential respirometer was used. For both species a set of 4 experimental flasks with 2 control flasks was run with KOH as the CO<sub>2</sub> absorbant. Each experimental flask contained 40 *Dendropoma corallinaceum* or 23 *Serpulorbis natalensis* in 2 mL filtered seawater. The control flasks were similar to the experimental flasks but lacked animals. The apparatus was kept at 15.5°C, close to the prevailing sea temperature and the flasks were gently shaken. After the animals were introduced, the ap-

paratus was allowed to equilibrate for 1 h. Readings were then taken every 3 h for a total of 15 h.

### BIOCHEMICAL ANALYSIS

Newly hatched juveniles were fixed in 5% saline formalin for transportation to the United Kingdom. The fixed samples of larvae complete with protoconchs were washed in 0.9% aqueous ammonium formate to remove seawater without changing the osmotic pressure, and freeze-dried. They were then comminuted in a vibrating ball mill. Carbohydrate and lipid contents were determined, as described previously by HOLLAND & HANNANT (1973). Protein was determined in a sample of the initial aqueous homogenate by the method of LOWRY, ROSEBROUGH, FARR & RANDALL (1951). Total dry weights were measured individually on a Cahn electrobalance after drying at 60°C for 48 h. Ash contents were weighed after roasting at 500°C for 4 h in platinum crucibles.

### RATES OF SINKING

In order to test potentiality of juveniles being carried by water currents, the rates of sinking of newly hatched juveniles were measured, using a 40 cm column of 38‰ seawater at 18°C and a stop-watch.

## RESULTS

### RESPIROMETRY

Respiration rates remained steady throughout the 15 h experiment with no evidence that O<sub>2</sub> became limiting.

At the termination of the experiment the young snails were still active and apparently healthy. The O<sub>2</sub> consumption rate corrected to STP was 0.11 µL per individual ( $4.26 \pm 0.25$  µL per flask) for *Dendropoma corallinaceum* and 0.07 µL per individual ( $1.66 \pm 0.07$  µL per flask) for *Serpulorbis natalensis*.

### BIOCHEMICAL ANALYSIS

Table 1 shows that about 35% of the total dry weight is due to protein. Carbohydrates account for less than 2% of the total dry weight. Neutral lipid, amounting to about 7 - 12% of the total dry weight, is the probable source of energy for the animals.

Newly hatched *Dendropoma corallinaceum* contain 5 µg neutral lipid, which is equivalent to 0.2 J energy (CRISP, 1971). Similarly, *Serpulorbis natalensis* contains 14.7 µg neutral lipid, equivalent to 0.06 J. Using an energy equivalent of 13.72 J mg<sup>-1</sup> O<sub>2</sub> STP liberated as heat during the catabolism of lipid (ELLIOTT & DAWSON, 1975), I estimate that *D. corallinaceum* loses  $2.16 \times 10^{-3}$  J h<sup>-1</sup> as heat and will therefore exhaust its lipid energy reserves in 4 - 5 days. *Serpulorbis natalensis* loses  $1.37 \times 10^{-3}$  J h<sup>-1</sup>, so that its lipid will last about 18 days. Catabolism of the carbohydrate would sustain *D. corallinaceum* for a further 5 - 6 h and *S. natalensis* for a further day.

### RATES OF SINKING

*Dendropoma corallinaceum* has a robust shell that sank at a rate of 3.2 cm sec<sup>-1</sup>, S.E. = 0.02, n = 5. *Serpulorbis natalensis* has a lighter shell and unlike *D. corallinaceum* is variable in size. The rate of sinking was inversely proportional to size, small individuals of 0.7 mm shell length

Table 1

Biochemical composition expressed as percentage of total freeze dried weight (including shell). Individual total dry weights are the means of 6 replicates. Figures in parentheses are the proportions of total lipid, total carbohydrate and protein in the biochemically extracted material.

	Individual total dry weight µg	Ash content %	Neutral lipid %	Phospholipid %	Free Polysaccharide %	Free sugars %	Protein %
<i>Dendropoma corallinaceum</i> newly hatched juveniles	73 ± 9	55	6.8 (22)	0.6	0.9 (4)	0.1	35.5 (76)
<i>Serpulorbis natalensis</i> newly hatched juveniles	126 ± 20	50	11.7 (24)	0.2	1.3 (3)	0.3	35.6 (73)



sinking at  $1.7 \text{ cm sec}^{-1}$ , S. E. = 0.01,  $n = 5$  and large individuals of  $1.4 \text{ mm}$  shell length sinking at  $1.0 \text{ cm sec}^{-1}$ , S. E. = 0.01,  $n = 5$ . The above sinking rates were observed for animals completely retracted within the shell. The sinking rate is reduced considerably when the animal extends its foot, and is reduced even further when a string of mucus is secreted. *Serpulorbis natalensis* reduced its sinking rate from  $1.7 \text{ cm sec}^{-1}$  with the foot retracted to  $0.7 \text{ cm sec}^{-1}$  with the foot extended. The sinking rate with a mucous "drogue" was very variable but was an order of magnitude less than the rates without mucus.

## DISCUSSION

Because of lack of time and equipment, only a few data on respiration rates and very crude data on energy reserves could be obtained. These data cannot be used as precise estimations but they do enable qualitative deductions to be made about the reproductive strategies employed by *Dendropoma corallinaceum* and *Serpulorbis natalensis*.

## ENERGY RESERVES

Lipid is the most efficient form of energy storage where size is limiting, as with the young of most marine invertebrates. Thus, HOLLAND *et al.* (1975) found that lipid is the major energy reserve of the veligers and developing embryos of *Littorina* spp. The same has been reported for oyster veligers (HOLLAND & SPENCER, 1973) and barnacle cyprids (HOLLAND & WALKER, 1975). The vermetids conform with this trend.

## DISPERSAL

*Dendropoma corallinaceum* will settle on adult colonies within 24 h after hatching but can delay settlement up to 4 days in the absence of suitable substrata. The adult feeding method using a mucous web probably occurs only after the completion of metamorphosis 2 days after settlement (HUGHES, 1978a). These published observations on settlement and the present data on respiration rates and lipid stores both predict that a maximum of 4-5 days is available to the juvenile *D. corallinaceum* for dispersal. Metamorphosis will take a further 2 days, during which time the lipid energy reserve will be virtually exhausted. However, *D. corallinaceum* tends to settle on Lithothamnium-type alga that grows over the rocks and over the surfaces of adult colonies. The settling juvenile rasps out a groove in the Lithothamnium to accommodate the grow-

ing shell, during which time green faecal pellets are produced. Evidently some of the eroded Lithothamnium is ingested and may provide supplementary food during metamorphosis. There are no data on the settlement behaviour of *Serpulorbis natalensis*. The above estimates are minimal, assuming that lipid is the principal energy source during dispersal and metamorphosis and taking no account of leaching of material during fixation. Carbohydrate is too scarce to be an important energy source and we suppose that protein is nearly all used for growth and enzyme production, although some energy is probably derived from protein catabolism. It is impossible to measure the absolute dispersal capabilities of either species in the field, but an indication of their relative dispersal powers can be derived from the data at hand. *Dendropoma corallinaceum* crawls at a speed of  $7.4 \text{ mm minute}^{-1}$ , which is twice as fast as *S. natalensis* (HUGHES, 1978a). The higher activity rate of *D. corallinaceum* is reflected by its higher respiration rate, being about 1.6 times that of *S. natalensis*. Thus, on a random walk, *D. corallinaceum* should be able to crawl  $\sqrt{2}$  times as far per day as *S. natalensis*. However, *S. natalensis* has energy reserves sufficient to last 4-5 times as long as *D. corallinaceum* and so should be capable of crawling much further than the latter species before settlement if suitable substrata are not encountered meanwhile.

The probability of any individual reaching a given distance will also depend on the mortality rate and cohort size. Little can be inferred about the mortality rates during dispersal except that *Dendropoma corallinaceum* lives on exposed shores where there is a danger of being dislodged by wave action, whereas *Serpulorbis natalensis* lives in calmer water below MLW and is less at risk to this danger. *Dendropoma corallinaceum* produces a single young per capsule, whereas *S. natalensis* releases about 24 young per capsule (HUGHES, 1978a). There is no information on relative development rates or on the lengths of breeding season (except that *D. corallinaceum* liberated young in the field during the entire study from July to November) but it seems likely that *S. natalensis* is much more fecund than *D. corallinaceum*.

So far we have assumed that juveniles disperse by crawling and are therefore limited to distances less than 10 m. It is possible that juveniles, having become detached from the substratum by wave action, are carried by water currents over much larger distances, depending on current speed and direction, turbulence and rate of sinking. The observed sinking rates show that *Dendropoma corallinaceum* must experience turbulence sufficient to carry even retracted individuals at least 10 m. Individuals with mucous drogues could be kept in suspension for several days and carried distances exceeding 100 or even 1000 m, de-

pending on currents. The sticky quality of the mucus would enhance reattachment should the disseminules be brought against a solid surface. However, the probability of a water-borne juvenile reattaching to a surface suitable for settlement must be very small, so that the majority of *D. corallinaceum* settling successfully will be those that have dispersed by crawling. Moreover, *D. corallinaceum* is highly gregarious, juveniles settling on any suitable place immediately outside the grazing ranges of the adults. Occasional individuals may succeed at long distance dispersal via water currents to found colonies elsewhere. The energy reserves will enable water-borne individuals to endure long distance dispersal, whereas quickly settling juveniles may be able to use the stored energy for more rapid metamorphosis and growth.

A similar general pattern of dispersal probably holds for *Serpulorbis natalensis*, except that smaller, looser colonies are formed. Long distance dispersal by water currents is possibly rarer; the calmer water will make detachment and suspension of the juveniles less frequent. Indeed, it is difficult to imagine how juveniles in calm water could become suspended. It is possible that *S. natalensis* sometimes produces planktonic veligers for long distance dispersal. The variability of hatching size has already been noted. HADFIELD *et al.* (1972) have shown for several Hawaiian vermetids that embryo size varies considerably within a species or even within single broods and that large embryos that have consumed more yolk from nurse cells hatch as crawling young, whereas smaller embryos that have consumed less yolk may be released as planktonic veligers.

## REPRODUCTIVE STRATEGIES

*Dendropoma corallinaceum* exploits a habitat that is severe because of heavy wave action, but is stable in the sense that environmental conditions remain constant throughout time. By forming continuous sheet-like colonies *D. corallinaceum* has become eminently suitable for exploiting the continually wave-scoured rock faces. Within its zone, *D. corallinaceum* is completely dominant, excluding all other species that potentially compete for space. This competitive superiority is achieved by the dense packing of contiguous individuals, which allows almost the entire surface of the colony to be grazed free of intruding organisms. However, once *D. corallinaceum* has extended to the limits of its zone, the space available to settling larvae will be confined to those micro-patches on the surface of the colony which are beyond the reach of the grazing adults (grazing occurs sporadically and is used primarily for clearing fouling particles rather than for feeding, which normally makes use of a mucous net).

New patches available for settlement will become available as adults die. Sections through colonies show that most individuals reach adult size, relatively few dying at small sizes. The colony is not built up in layers but increases in thickness due to the upward spiral growth of adults and of juveniles that have settled gradually and sporadically over the surface of the colony. Space suitable for settling juveniles must be severely restricted and probably becomes available at a slow steady rate. The best strategy under these circumstances is to liberate gradually, over a protracted period, large juveniles that are robust and advanced enough to settle, metamorphose and grow quickly. The production of many juveniles, especially in pulses, would be disadvantageous because most of them would fail to find a vacant settlement site. Moreover, with a fixed parental energy income, the production of more young would reduce their individual size and hence their competitive ability. *Dendropoma corallinaceum* is a good example of a K-selected species (MACARTHUR, 1972) adapted to stable environmental conditions where the population remains close to an equilibrium density and competition (for space) is at a premium. As expected from the theory of r- and K-selection, *D. corallinaceum* has a protracted breeding season (at least from July to November), relatively low fecundity, but large young. These K-selected attributes are achieved at a cost of lowered potential rate of increase and dispersability. Unpredictable, density-independent mortality does strike *D. corallinaceum*. Old colonies that have become very thick are weakened and tend to slough off the rock in small patches. The effect is exacerbated by subsequent wave action that erodes the newly exposed edges of the colony. Dispersal to such newly bared rock is well within the capabilities of juveniles crawling from the surrounding colonies. However, settlement in such bare areas was never recorded in the field, probably because the rocks in the study area were too hard for the juveniles to rasp the shallow groove that is necessary for their successful attachment (HUGHES, 1978a, 1978b). Settlement only occurs on the surface of colonies or on patches of *Lithothamnion*-type calcareous algae that occur both on rocks and among the shells of established colonies. Long distance dispersal would therefore seem relatively unimportant. However, *D. corallinaceum* has a wide geographical range within which suitable rock faces are often separated by large tracts of unsuitable coastline. Occasional long distance dispersal in water currents must take place and an adequate mechanism for it is provided by the mucous "drogue."

*Serpulorbis natalensis* forms loose colonies that never monopolise space on the substratum but grow among a large variety of other sedentary organisms. The undersur-



faces and sides of stones and boulders no doubt provide a microenvironment that is less stable than the wave-swept rock faces colonised by *Dendropoma corallinaceum*. Periods of very rough weather, subtle changes in prevailing water currents and deposition of silt, or the encroachment of other sedentary organisms are factors that might cause unpredictable fluctuations in the microenvironment. Competitive ability (for space) can be increased either by forming dense colonies where individuals benefit from the anti-fouling activities of their neighbours (*D. corallinaceum*) or by remaining separate from neighbours but growing to a larger individual size (*S. natalensis*). The dense colonial structure works well in a stable habitat and where microenvironmental quality remains the same over large patches of substratum. In more unstable habitats or on more heterogeneous surfaces, *e.g.*, where microenvironmental quality changes from boulder to boulder or even within boulders, it would be better to have more widely dispersing offspring. The more isolated individuals would then have to depend on size rather than coloniality in the competition for space with other organisms. Larger size allows greater fecundity, which itself would compensate for the greater mortality accompanying wider dispersal.

## SUMMARY

Newly hatched *Dendropoma corallinaceum* weighed about 37  $\mu\text{g}$  total dry weight (including protoconch) of which 35.5% was protein, 1% was carbohydrate and 7.4% was lipid, suggesting that lipid was an important energy source during the dispersal phase. At 15.5°C (ambient sea temperature) the crawling young used 0.11  $\mu\text{L O}_2 \text{ h}^{-1}$  so that the energy reserves would last 4-5 days. Newly hatched *Serpulorbis natalensis* weighed about 126  $\mu\text{g}$  total dry weight with a biochemical composition fairly similar to that of *D. corallinaceum*. At 15.5°C the crawling young used 0.07  $\mu\text{L O}_2 \text{ h}^{-1}$  so that the energy reserves would last 18-19 days.

*Dendropoma corallinaceum* respired and crawled at twice the rate for a similar sized *Serpulorbis natalensis*; however, the potential maximum distance crawled prior to settlement may be much greater for *S. natalensis*, which has larger energy reserves. The majority of juveniles of both species probably disperse by crawling and settle near

the parents, but a few may undergo long distance dispersal buoyed up by using water currents and a mucous thread.

*Dendropoma corallinaceum* is a "K-selected" species adapted for high competitive ability in a temporally and spatially predictable environment. Accordingly it produces relatively few, large young over a protracted breeding season. *Serpulorbis natalensis* is a more fecund, wider dispersing species adapted to a more heterogeneous and perhaps less stable environment.

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